THE SANTA CRUZ TYPOTHERIA.

(Figures 1–10.)

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(*Read April 24, 1908.*)

The Typotheria are a group of semi-ungulate mammals of strictly South American origin appearing first in the Notostylops beds of Patagonia.[1] During the Santa Cruz epoch four genera are represented but what is lacking in generic and specific diversity is more than compensated for by an abundance of individuals. The total number of common species apparently does not exceed eight, but this

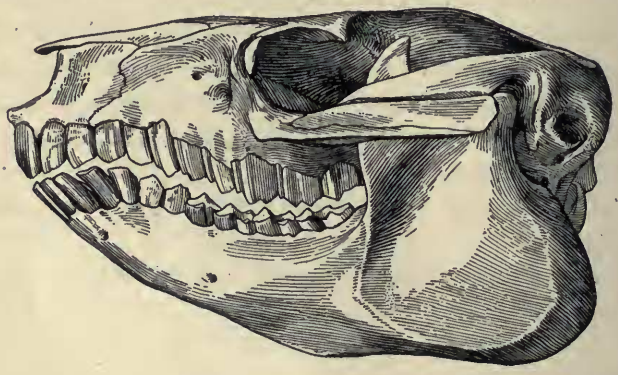

Fig. 1. Skull of *Protypotherium australe* Ameghino, side view, three fourths the natural size. (No. 9565 American Museum of Natural History collection.)

has been increased to no less than fifty-one by failing to estimate at their true value characters due to age and others which seem to be of the nature of individual variations in size, the result no doubt of the extremely fragmentary character of the material hitherto available. Even with the large suites of specimens in the collections

[1] *Isotypotherium, Epitypotherium.*

at Princeton University and the American Museum of Natural History it has been found impossible to separate in a satisfactory manner the species of the genus *Protypotherium*. An almost exact intergradation in size without appreciable difference in structure is observable between the largest species *Protypotherium australe* (Fig. 1) and the smallest *P. attenuatum*. As none of the collections have been made with strict regard to stratigraphic sequence, we are not in a position to say whether these differences represent individual variations or true mutations. The former alternative has been adopted in monographing the group (see the forthcoming Volume VI., Part I. of the "Reports of the Princeton University Expeditions to Patagonia").

Classification of the Santa Cruz Typotheria.

The Typotheria are grouped by Scott[2] as a suborder of the Toxodontia and may be defined as follows:

Plantigrade or digitigrade mammals with pentadactyl[3] or tetradactyl feet, strongly interlocking carpus with os centrale and serial or slightly interlocking tarsus with hemispherical astragalar head. Dentition usually complete but tending toward reduction of the lateral incisors, canine and anterior premolars in specialized forms. Median incisors more or less enlarged and functional as cropping teeth. Molars hypsodont, lophoselenodont in crown pattern, curving inward above and outward below. A clavicle is present in some forms. Femur with third trochanter. Fibula articulating with calcaneum.

Two well-marked families are recognizable among the Santa Cruz representatives of the suborder for which the names Interatheridæ and Hegetotheridæ have priority. Each contains a large and a small genus of which, in either case, the former is the less specialized. The following key to the families and genera may facilitate the determination of new material:

[2] Scott, W. B., "The Miocene Ungulata of Patagonia," *Rept. British Asso. Adv. Sci.*, 1904, pp. 589–590.

[3] Ameghino figures a pentadactyl manus in *Pachyrukhos typicus*, "Contrib. al conocimiento de los mamíferos fósiles de la República Argentina," *Actas de la Academia Nacional de Ciencias en Córdoba*, T. V., Pl. 13, fig. 14, 1889, and in *Typotherium*, *ibid.*, Pl. 18, fig. 5.

Order *TOXODONTIA* Owen.

Suborder TYPOTHERIA Zittel.

A. Family Interatheridæ. Median incisors rooted; third and fourth premolars not completely molariform, squamoso-mastoid region dilated and cancellous; malar long and narrow, inclosed between temporal process of maxillary and squamosal; maxillary orbital; carotid canal and foramen lacerum posterius fused; tibia and fibula unfused distally; pes paraxonic, digits II. and V. equally reduced and small, digits III. and IV. large and of equal length; astragalar trochlea bilaterally symmetrical; no naviculo-calcaneal facet; calcaneum with large fibular facet.

1. *Protypotherium.* Dental formula $\frac{3}{3}, \frac{1}{1}, \frac{4}{4}, \frac{3}{3}$ in close series. Lateral incisors unreduced; canine incisiform; upper molars with deep internal inflection and slight antero-external ridges; M_3 externally bilobate; temporal bar of maxillary with slight descending process; humerus with internal epicondylar foramen; terminal phalanges laterally compressed hoofs with slight clefts in manus.

2. *Interatherium.* Dental formula $\frac{3}{3}, \frac{1}{1}, \frac{4}{4}, \frac{3}{3}$, with diastemata between the lateral incisor, canine and first premolar, varying with the species. I^2 reduced, often wanting; upper molars with deep internal inflection and prominent antero-external ridges; M_3 externally trilobate; temporal bar of maxillary with strong descending process; humerus without internal epicondylar foramen; terminal phalanges laterally compressed hoofs with or without clefts.

B. Family Hegetotheridæ. Median incisors rootless; third and fourth premolars molariform; mastoid dilated inclosing a large hollow cavity; malar large excluding maxillary from orbit; carotid canal and foramen lacerum posterius widely separated; tibia and fibula firmly fused both proximally and distally; pes approaching mesaxonic with digit III. the longest, digit V. greatly reduced and digits II. and IV. shorter than III. but robust; astragalar trochlea bilaterally asymmetrical; navicular and calcaneum in articulation; small fibulo-calcaneal facet.

1. *Hegetotherium.* *Dental formula* $\frac{3}{3}, \frac{1}{1}, \frac{4}{4}, \frac{3}{3}$. Second and third upper and third lower incisor vestigial; canine vestigial; upper molars internally convex, without inflection except in M^2; ectoloph smooth; terminal phalanges greatly flattened transversely with prominent clefts.

2. *Pachyrukhos.* Dental formula $\frac{1}{2}, \frac{0}{0}, \frac{3}{3}, \frac{3}{3}$. All the upper molars internally convex; ectoloph smooth; terminal phalanges hoof-like without clefts in Santa Cruz species.

The Santa Cruz typotheres are animals of somewhat rodent-like appearance, varying in size from a cotton-tail rabbit to a cavy. A review of the more important skeletal characters of the group may be of value, even though it involve some repetition.

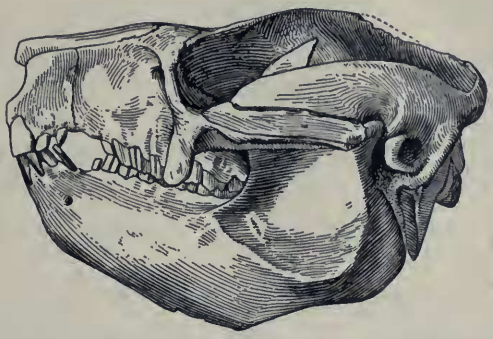

FIG. 2. Skull of *Interatherium robustum* Ameghino, side view, three fourths the natural size. (No. 9263 American Museum of Natural History collection.)

1. *The Skull.*—The facial portion of the skull is slender and more or less excavated longitudinally while the brain case is broad and well expanded. The orbits are central, circular in outline, quite prominent in *Hegetotherium, Pachyrukhos* and *Interatherium* and unenclosed posteriorly. The jugal arches are robust in all except

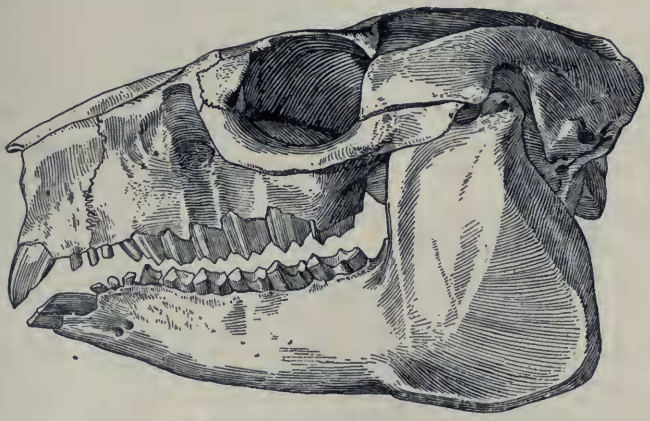

FIG. 3. Skull of *Hegetotherium mirabile* Ameghino, side view, three fourths the natural size. (No. 15542 Princeton University collection.)

Pachyrukhos and moderately expanded. The premaxillæ are short and heavy with scarcely any ascending process; the nasals are broad posteriorly, tapering forward to blunt points; the interorbital tract plane and the sagittal and lambdoidal crests low. The most promi-

nent feature of the back of the skull is the greatly distended mastoid tract which may either be filled with cancellæ or lodge a large cavity. In either case there is direct communication with the tympanic bulla and the dilation appears to have functioned as a secondary resonator, perhaps associated with nocturnal habits. The palate is concave throughout, terminating posteriorly in a pair of stout processes. The mandible is heavy and deep, without trace of suture in the firmly fused symphysis.

2. *Dentition.*—Beginning with the normal incisor formula in *Protypotherium* (Fig. 1) the Santa Cruz typotheres show a well-marked tendency toward an increase in size of the median incisors at the expense of the lateral incisors, canine and anterior premolar until the extreme stage of reduction in *Pachyrukhos* (Fig. 4) is attained. The teeth undergoing elimination are reduced to simple cylinders. It is not to be understood that *Protypotherium, Interatherium, Hegetotherium* and *Pachyrukhos* constitute a phyletic series because they represent successive stages in the process of dental reduction associated with the hypertrophy of the median incisors. As already indicated in the key to the genera, two divergent lines are represented and not a single progressive series. A rather curious feature of the lower incisors in *Protypotherium* is the presence in the first and second of a deep median cleft producing a fork-like structure recalling a somewhat similar division of the lower incisor crowns in the Hyracoidea. In all the Santa Cruz typotheres the enamel layer on the enlarged incisors tends to be confined to the anterior surface of the crown. The molars in all the genera are constructed on much the same plan but only in *Protypotherium* are absolutely unworn teeth known, consisting essentially of a broadly concave ectoloph (*e*, Fig. 8, *A*) and a pair of crescents with the convexity directed inward (*ac, pc,* Fig. 8, *A*), of which the anterior horns are fused with the ectoloph inclosing a reentrant. A crista-like ridge from the ectoloph (*c,* Fig. 8, *A*) is separated from the anterior crescent by a deep notch. A slight ridge (*pp,* Fig. 8, *A*) blocks the shallow valley inclosed by the posterior crescent. As the tooth wears the antero-external angle of the crown elongates and is channeled by a shallow groove producing the ridges noted in the key to the genera.

In the lower molars the convexity of the crescents is reversed so that the reentrant fold is external (Figs. 1, 3, 9, *A*). A prominent lobe spanning the arc of the posterior crescent (*pp*, Fig. 9, *A*) is not peculiar to the teeth of the Typotheria alone, but is present also in *Nesodon* (Fig. 9, *B*), *Astrapotherium, Theosodon* and other extinct ungulates from South America. In the last lower molar the development of the third lobe present in *Interatherium* is accomplished by the deepening of the shallow groove indicated in *Protypotherium* at the point marked *pc* in Fig. 9, *A*.

As mentioned in the generic key the premolars are sometimes molariform and sometimes not, differing from the molars in the latter case in having the anterior crescentic lobe smaller than the posterior.

Roots are developed only in the deciduous molars but as these have been observed only in *Protypotherium* and *Interatherium* it is

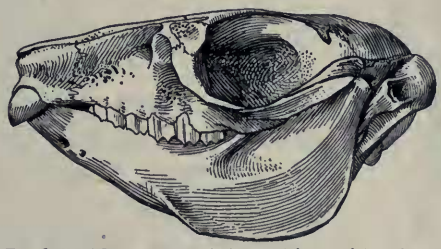

FIG. 4. Skull of *Pachyrukhos moyani* Ameghino, side view, three fourths the natural size. (Reconstructed from several specimens.)

not altogether certain whether this character is of family or subordinal value. So far as can be ascertained the crown pattern seems to have been the same in the deciduous and permanent series, the milk teeth resembling their successors. The order of replacement seems to have been the normal one.

A thin layer of cement is usually observable on the molars and premolars of all the genera.

3. *Axial Skeleton.*—The dorso-lumbar vertebral formula in *Interatherium* is twenty-two, of which fifteen are dorsals. It was probably the same in *Protypotherium* but in *Pachyrukhos* eight lumbars are present. Five vertebræ are coössified, in the sacral complex of which three are true sacrals in contact with the ilium and

two belong to the caudal series. The length of the tail seems to have varied. In *Protypotherium* and *Interatherium* it is both long and heavy while in *Pachyrukhos* there is reason to believe that it was quite short.

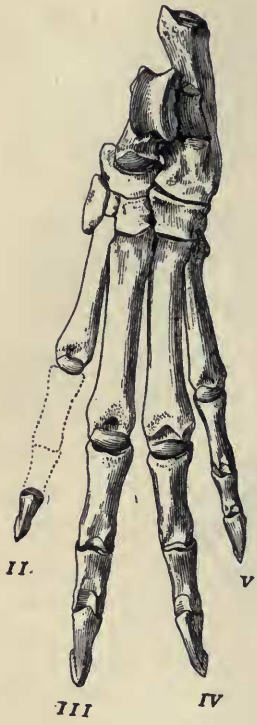

FIG. 5. Left hind foot of *Protypotherium australe* Ameghino, three fourths the natural size. (No. 9149 American Museum of Natural History collection.)

4. *Foot Structure.*—Almost nothing has hitherto been known of the structure of the feet in the Santa Cruz typotheres, but definite information is now available for all the genera except *Hegetotherium,* in which the manus is still unknown, but from the close structural resemblance of *Hegetotherium* and *Pachryukhos* it is probable that it was not unlike that of the latter, which in turn does not differ materially from the manus of *Interatherium* and *Protypotherium* (Fig. 6, *A*). In the Santa Cruz forms both manus and pes are tetradactyl without the slightest trace of an opposable thumb or great toe.[4] The carpus is strongly interlocking and shows no trace of the centrale. Two types of hind foot are developed (Figs. 5 and 7, *A*) simulating the paraxonic and mesaxonic symmetry of the feet of the Artiodactyla and Perissodactyla. These are probably to be correlated in the Typotheria with cursorial and saltatorial modes of progression. *Pachyrukhos* was certainly a jumping animal as shown by the greater length and strength of the hind limbs and inner digits of the pes. In fact, the structure of both the fore and hind limbs in this animal

[4] A pentadactyl manus with separate centrale in the carpus and opposable thumb and a pentadactyl pes with large opposable hallux figured by Ameghino, *Revista Argentina de Hist. Nat.,* I., pp. 393, 394, figs. 95, 96 and referred to *Interatherium* (*Icochilus*) *robustum* do not pertain to this genus. The same figures with the erroneous determination appear also in Zittel's "Handbuch der Palaeontologie," IV., p. 493, fig. 407.

closely resembles that of the rabbit. From the numerous structural similarities between *Pachyrukhos* and *Hegetherium* it may be inferred that the latter was also saltatorial. Its broad, shallow astragalar trochlea is in contrast with the narrow, more deeply incised trochlea of the cursorial *Protypotherium* and *Interatherium*. Both of these genera have the fore and hind limbs of approximately equal length. The terminal phalanges in the Santa Cruz typotheres are hoof-like and in *Hegetotherium* have prominent median clefts.

Relationships of the Santa Cruz Typotheria.

1. *With the Toxodonta.*—In the evolution of the teeth and feet, the Santa Cruz Typotheria are less advanced than their contemporaries, the Nesodons. The feet of *Nesodon* (Figs. 6, *B*, 7, *B*) are

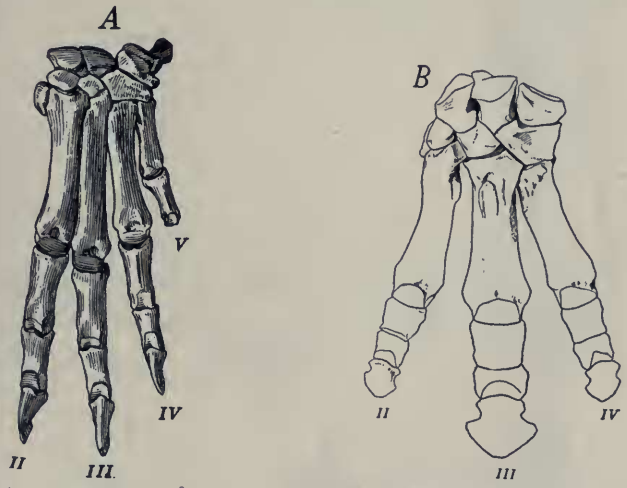

Fig. 6. *A*. Left fore foot of *Protypotherium australe* Ameghino, three fourths the natural size. (No. 9149 American Museum of Natural History collection.) *B*. Left fore foot of *Nesodon imbricatus* Owen, about one fifth the natural size. (No. 15460 Princeton University collection.)

tridactyle with the axis passing through the third digit. The manus has originally been tetradactyl like that of *Protypotherium* (Fig. 6, *A*) but has lost almost all trace of the fifth digit, a mere vestige, not shown in the figure, remaining. The other bones of the wrist and foot have not suffered any displacement as a result of this loss but interlock in the same way as in *Protypotherium*. The hind foot

of *Nesodon* (Fig. 7, *B*) is the realization of a structure already foreshadowed in the pes of *Hegetotherium* (Fig. 7, *A*). The fifth digit, which is greatly reduced in *Hegetotherium,* has here disappeared and the ento- and meso-cuneiforms have united to a single bone. The shortening of the neck of the astragalus and the increase in size of the fibular facet on the calcaneum are, perhaps, adaptations to the support of weight. Although the molars of *Nesodon* appear

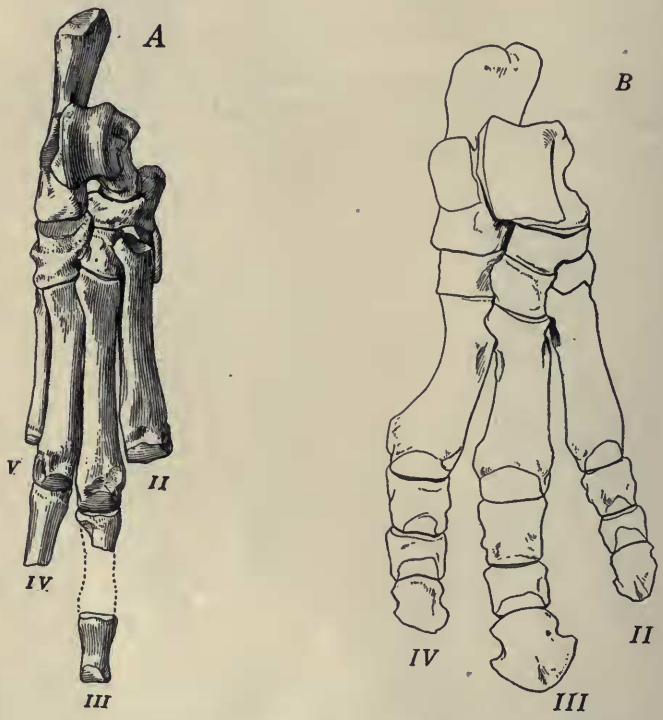

FIG. 7. *A. Hegetotherium mirabile* Ameghino, right hind foot, three fourths the natural size. (No. 15542 Princeton University collection.) *B. Nesodon imbricatus* Owen, right hind foot, about one third the natural size. (No. 15460 Princeton University collection.)

exceedingly complex, owing to the development of secondary enamel folds, the primary elements can be homologised with those displayed in the simpler crown pattern of *Protypotherium,* as indicated by the similar lettering in Figs. 8 and 9. This comparison can not yet be

extended to the other Santa Cruz genera, *Hegetotherium, Pachyrukhos* and *Interatherium,* as unworn molars of these are not available. *Nesodon* differs from the Typotheria in the enlargement and caniniform character of the second incisor above and the third below, while in the Typotheria the median incisor in both jaws is the only one tending toward great increase in size. In none of the Santa Cruz Typotheria is there a trace of the double deciduous dentition characteristic of *Nesodon.*

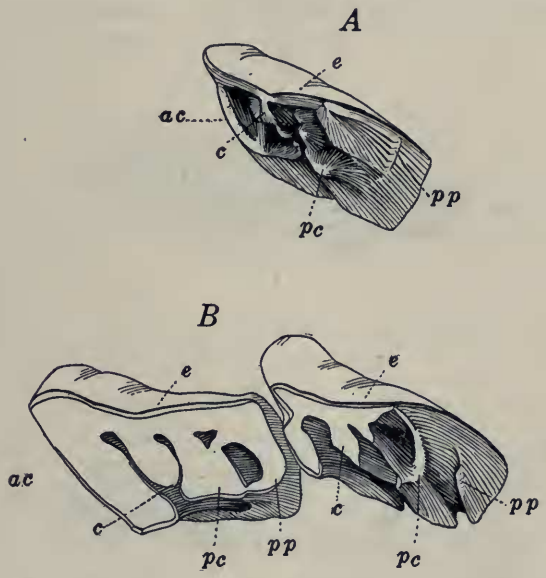

FIG. 8. *A.* Unworn third upper molar of a young *Protypotherium,* four and one half times the natural size. (No. 9482 American Museum of Natural History collection.) *B. Nesodon imbricatus* Owen, second and third upper molars slightly worn, three fourths the natural size. (No. 15135 Princeton University collection.) *ac,* antero-internal crescent; *pc,* postero-internal crescent; *e,* ectoloph; *c,* crista; *pp,* posterior pillar.

From these resemblances in dentition and foot structure it seems permissible to infer that the Toxodonta and Typotheria had a common origin, but the facts at present available do not justify us in saying more.

2. *With Typotherium.*—Difficult as it is to ascertain the relationship existing between the Santa Cruz Typotheria and the Nesodons,

it is even more so to determine their degree of kinship with *Typotherium.* From their small size it seems quite probable that none of the Santa Cruz Typotheria are in the direct line of descent culminating in this genus. This is confirmed by the degree of specialization in dentition and foot structure which *Typotherium* displays. The teeth of the latter show a greater complexity of folding than is attained by any of the Santa Cruz typotheres, while the feet are less specialized with a pollex in the manus which has been lost in *Protypotherium,* the most generalized of the Santa Cruz typotheres

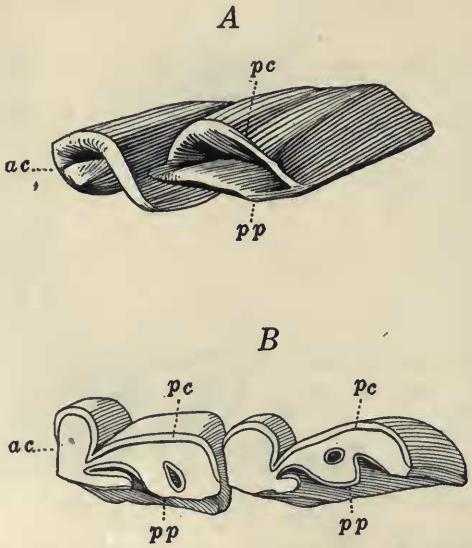

Fig. 9. *A.* Unworn third lower molar of a young *Protypotherium,* four and one half times the natural size. (No. 9482 American Museum of Natural History collection.) *B. Nesodon imbricatus* Owen, two lower molars, three fourths the natural size. (No. 15135 Princeton University collection.) *ac,* anterior crescent; *pc,* posterior crescent; *pp,* posterior pillar.

(Fig. 6, *A*), and with digit V. of the pes less reduced than in the most specialized of the latter (*Pachyrukhos*). A pollex has been figured by Ameghino[5] in the manus of *Pachyrukhos typicus,* but none has been found in any Santa Cruz specimen. The manus in *Hegetotherium* is unknown, so the above statement regarding the

[5] Ameghino, Florentino, "Contrib. al conoc., etc.," Pl. 13, fig. 14.

degree of specialization in foot structure displayed by *Typotherium* may require some modification in the light of fuller knowledge.

3. *With the Rodents.*—In many features of skull and skeleton the Typotheria resemble the rodents. This is most apparent in *Pachyrukhos,* which seems to have been a saltatorial animal, but in none of the Typotheria are the following characters peculiar to rodents developed:

A. Persistently growing, chisel-shaped incisors (I. $\frac{2}{2}$ of the permanent series, Weber).[6] I. $\frac{1}{1}$ of the permanent series is enlarged in some of the Typotheria and may grow persistently but is modified for cropping and not for gnawing.

B. More or less antero-posterior elongation of the mandibular condyle and corresponding modification of the glenoid fossa to permit backward and forward movement of the lower jaw. In the Typotheria the condyle is approximately circular in outline with the glenoid surface flattened and the movement of the mandible is from side to side.

C. Frequent outward curvature of the crowns of the upper molars and inward curvature of those of the inferior series in hypsodont forms. The reverse is true in the Typotheria.

D. Contact of ascending process of premaxillary with frontal. This process is short and robust in the Typotheria and is widely separated from the frontal by the maxillary.

E. Elongation of the mandibular angle. The angle is evenly convex in the Typotheria.

F. The astragalus in rodents is characterized by a broad, short, rather shallow trochlea with the crests sharp and equally developed, distinct neck and flattened head, convex distally; trochlea symmetrical to the vertical plane; fibular and internal malleolar facets vertical; body limited posteriorly; no astragalar foramen. In the Santa Cruz Typotheria the body is deeper than in rodents, the crests may or may not be equally developed and the head is globular without antero-posterior flattening. The symmetry of the trochlea with respect to the vertical plane varies in the different families. In the other characters they resemble rodents.

[6] "Die Säugetiere," p. 480, 1904.

G. The presence of a free centrale in the carpus in all rodents except the Hystricidæ and *Caelogenys* and the general fusion of the scaphoid and lunar in all except the Bathyergidæ, Ctenodoctilidæ and Lagomorpha.[7] The centrale is wanting in the carpus of the Typotheria and the lunar is always free.

H. The presence of a tibial sesamoid in all the simplicidentate rodents. This is not found in the tarsus of the Typotheria.

The Typotheria resemble rodents in the elongation of the anterior portion of the skull with the reduction of the incisor-canine-premolar series (*cf.* Figs. 3 and 4), in the enlargement and often permanent growth of the median incisors (not homologous with the enlarged incisors in rodents, see under *A,* above), in the development of a mastoid dilation which may be filled with cancellæ (Interatheridæ) as in many rodents and connected with the auditory bulla, in the shape of the proximal articular surfaces between the radius and ulna, in the broad anteriorly directed transverse processes of the lumbar vertebræ and in several other characters of minor importance.

Fig. 10. Left hind foot of *Procavia* (*Dendrohyrax*) *arborea,* ¾ natural size. (No. 365 Princeton University osteological collection.)

In view of the striking differences in structure indicated in the preceding paragraphs, it seems probable that these resemblances are to be explained as instances of convergence.

4. *With the Hyracoidea.*—A more or less intimate relationship between the Typotheria and Hyracoidea is commonly assumed but with the complete material now available it is difficult to see on what grounds this hypothesis can be maintained. The hyracoid carpus is arranged on the linear plan with separate centrale while in the tarsus the astralagus is unlike that of any other mammal in possessing a large step-like articulation for the internal tibial malleolus (Fig. 10).

In striking contrast with hyrax, the carpus in the Typotheria is strongly interlocking without centrale, and the internal tibial malleolus is applied to the lateral surface of the astragalus without trace

[7] Weber, *loc. cit.,* p. 476.

of the supporting shelf (Figs. 5 and 7, *A*). The flat astragalar head in the Hyracoidea and the articulation of the fibula with the astragalus instead of with the calcaneum are additional points of difference, all of which are more than sufficient to offset similarities in skull structure which are confined to a few points, such as the cancellous dilation of the mastoid, the shape of the posterior border of the palate, and the increase in depth posteriorly of the mandible. In the Hyracoidea the molar takes part in forming the outer portion of the glenoid cavity, the parietal enters into the postorbital process and the base of the coronoid just back of the last lower molar is perforated by a large foramen, a superior branch of the alveolar canal. None of these characters are exhibited by the Typotheria. In the hyracoid dentition, the first upper incisor is a persistently growing downwardly curved tusk of triangular cross-section. In some of the Typotheria this tooth may grow persistently but it is always antero-posteriorly compressed, transversely expanded and modified for cropping, never appearing as a tusk. The molars of the Hyracoidea are lophoselenodont and either brachyodont or short hypsodont while in the Typotheria they are extremely hypsodont, developing roots only in the deciduous series. The crown pattern of the hyracoidean molar bears more resemblance to that of some of the early horses and rhinoceroses than to the molar pattern in the least specialized of the typotheres (Figs. 8 and 9).

The so-called hyracoids from the Fayum Province of Egypt (*Saghatherium, Megalohyrax*) are as yet known only from fragments of the skull and dentition but, so far as the available material permits comparison, resemble the modern Hyracoidea and not the Typotheria which would probably not be the case if the two orders were related as it would naturally be expected that a closer similarity should exist between the Eocene and Miocene representatives of an order than between the latter and the recent forms. All the Egyptian hyracoids have the base of the coronoid perforated by a branch of the dental canal as in the recent forms[8] and unlike the Typotheria.

[8] Communicated by Mr. Walter Granger, of the American Museum of Natural History.

Various pre-Santa Cruz genera (*Archæohyrax, Argyrohyrax*) have been referred to the Hyracoidea. Their foot structure is still unknown but the skull and dentition, to judge from the photographs, figures and descriptions examined by the writer, are not hyracoidean in character. Too little is known of these forms to warrant a discussion of their relationship with the Santa Cruz Typotheria, but there can be little doubt that they should be referred to the same suborder.

Princeton University, April, 1908.